

**An unusual dendrodorid: redescription of the tropical nudibranch
Dendrodoris atromaculata (Alder & Hancock, 1864)
(Anthobranchia: Doridoidea: Dendrodorididae)**

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ABSTRACT

Dendrodoris atromaculata (Alder & Hancock, 1864) is a large, tropical nudibranch mollusc living in the Indo-west Pacific Ocean. A detailed description of the external morphology of the living animal and an investigation of internal anatomy are presented for the first time. In addition the microstructure of certain organs (i.e., notal tissue and the vestibular gland associated with the reproductive system) are compared with other *Dendrodoris* species. *Dendrodoris atromaculata* is unique among currently described species of *Dendrodoris* in three respects, the gill structure is “cross-like”, the notum possesses prominent spicules and the notum is covered in finger-like processes. These findings necessitate a reassessment of previously documented generic features of *Dendrodoris* and reveal a need for changes to future phylogenetic analyses of both porostome and cryptobranch dorids.

Key words: nudibranch, *Dendrodoris*, Dendrodorididae, histology, radula-less

INTRODUCTION

Indo-Pacific members of the genus *Dendrodoris* are in need of taxonomic review (Rudman 1998; Valdés & Gosliner 1999). At least twelve members of the genus are found in Australian waters (Brodie 2002). Several of these species, i.e., *Dendrodoris maugeana* Burn, 1962 and *D. carbunculosa* (Kelaart, 1858), are relatively rare and this has hindered interspecific comparison. An investigation of another such rare species follows; it provides new information of the morphological and anatomical characteristics of *D. atromaculata* (Alder & Hancock, 1864) a large tropical nudibranch first described from the south-eastern coast of India, and barely mentioned in the literature since (see Eliot 1906a; Willan & Coleman 1984).

Unlike the majority of nudibranchs, members of the genus *Dendrodoris* lack both a radula and jaws (Young 1969). In addition members of the genus are not easily recognised as a cohesive group by their external features alone, placing increased emphasis on internal investigations for identification. The internal anatomy of *D. atromaculata* has never been investigated prior to the current study.

In the past, research on the features of *Dendrodoris* have been confounded by a mistaken synonymous relationship with the genus *Doriopsilla* (e.g., Steinberg 1961; Thompson 1975; McDonald 1983). However more recently, Perrone (1986), Valdés *et al.* (1996) and Valdés & Ortea (1997) [all working on Atlantic or Mediterranean species] clearly established that, unlike members of the genus *Doriopsilla*, members of the *Dendrodoris* possess oral (ptyaline) glands that are well-separated from the digestive system.

Valdés *et al.* (1996) and Brodie *et al.* (1997) agreed that the gill structure of members of *Dendrodoris* was circular and often closed posteriorly by the anus.

In a detailed phylogenetic analysis of radula-less (porostome) dorids (Valdés & Gosliner 1999) found no members of the genus *Dendrodoris* to possess notal spicules (= integumentary spicules of Valdés & Gosliner 1999). Such spicules were also considered absent from the *Dendrodoris* species used in a recent phylogenetic analysis of cryptobranch dorids (see Valdés 2002). In addition, finger-like mantle papillae were not considered in either of the above studies. This maybe significant because, along with notal spicules, this feature is found in the outgroup genus *Bathydoris* (see Wägele 1989). It is therefore vital to document these unusual features in *D. atromaculata* and to gain a broader perspective of the morphological variation found within the taxon *Dendrodoris*.

MATERIALS AND METHODS

Live specimens of *D. atromaculata* were collected intertidally at Nasese, Suva, Fiji and Rowes Bay, Townsville, Australia by the author and also intertidally in Townsville by members of the undergraduate Marine Invertebrate Biology class at James Cook University. These specimens are prefixed as BC (Brodie Collection) and will be lodged as voucher specimens with the Museum of Tropical Queensland, Townsville. Additional preserved specimens, including the type material, and photographic material were obtained from the following institutions: Hancock Museum, Newcastle-on Tyne, UK (NEWHM); Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM); and the National Museum of Victoria, Melbourne, Australia (NMV).

After observation in the laboratory, live animals from Rowes Bay were preserved in 8 % formalin in seawater for several weeks. They were then dissected and the anatomical details of organ systems (e.g., reproductive system and gut) were documented using a camera lucida. Organ systems intended for histological analysis were dehydrated, using increasing concentrations of ethanol, before being embedded in hydroxyethylmethacrylate resin (Technovit 7100 by Kulzer, Wehrheim). Sections (3 µm thick) were obtained using a

powered microtome (Model 1140/Autocut, Reichert-Jung Universal, München) equipped with a tungsten-carbide knife. The ease of sectioning improves if blocks are prepared several weeks prior to use. Sections were stained with toluidine blue, a metachromatic stain (Winsor 1994) that stains acid mucopolysaccharides in various shades of red to violet, while neutral mucopolysaccharides are stained blue (see Wägele 1998).

Additional wax embedded sections, of notal tissue and a vestibular gland from the reproductive system, were Gram stained according to Twort (see Bancroft & Stevens 1977) to search for the presence of bacteria and PAS stained (see Bancroft & Stevens 1977) to test for the presence of fungi. These tests were undertaken for two reasons (1) because bacteria have been found in the vestibular gland of other members of the genus *Dendrodoris* (see Klusmann-Kolb & Brodie 1999) and (2) because unknown structures resembling fungi were observed in the thin-section resin samples taken from the notum (Brodie unpublished data). If present, fungi stain PAS+ (= magenta). Unless specified otherwise all references to colour in the histological results refer to staining with toluidine blue.

A whole mounted penis of *D. atromaculata* (from a specimen from Rowes Bay) was stained with Eosin (see Bancroft & Stevens 1977), then dehydrated with increasing concentrations of ethanol, before clearing in xylene and mounting in DPX (BDH, Poole). The penis was then examined using a Confocal Laser Scanning Microscope (Nikon Eclipse 6600).

RESULTS

Taxonomy

Order Nudibranchia Blainville, 1814

Suborder Anthobranchia Férussac, 1819

Superfamily Doridoidea Odhner, 1934

Porostomata Bergh, 1981

Family Dendrodorididae O'Donoghue, 1924

Genus *Dendrodoris* Ehrenberg, 1831 [Type species *D. lugubris* subs. desig. by Gray, 1847]

***Dendrodoris atromaculata* (Alder & Hancock, 1864)**

(Figures 1A-F & 2A-D)

Synonymy

Doridopsis atromaculata Alder & Hancock, 1864, p. 129, Pl. XXXI. figs. 20 - 24.

Dendrodoris atromaculata (Alder & Hancock). — Eliot 1906a, p. 662; Willan & Coleman 1984, p. 53.

Dendrodoris sp. 2 Lim & Chou 1970, 96-97, figs. 4N & 9C.

Dendrodoris singaporensis Lim & Chou 1970, p. 104.

Comments on Synonymy

The genus *Dendrodoris* was created by Ehrenberg (1831) for a dorid from the Red

Sea, which was neither adequately described nor dissected, and thus the name was neglected for almost a century (Gohar & Soliman 1967). Later, Alder and Hancock (1864) founded an equivalent genus *Doridopsis* on Indian Ocean material. Although *Dendrodoris* was the first genus name used to collectively describe radula-less dorids, the name *Doridopsis* was often used because its original description was superior. Pruvot-Fol (1930) provided clarification when she showed that *Doridopsis* was unequivocally synonymous with *Dendrodoris*. She then advocated the use of the name *Dendrodoris* (instead of *Doridopsis*) because of its chronological priority.

The original description of *D. atromaculata* was short, based on preserved material, and contained information about external features only. However, the description was accompanied by excellent drawings that leave no doubt that the material examined in the current study is the same species. Features of particular note in the description, that clearly match it to the current material, are the high convex body, overall colour and markings and the irregular “star-like” surface of the tubercles. The combination of these three features being unique within the Doridoidea.

Dendrodoris atromaculata was redescribed by Eliot (1906a) based on reinvestigation of the preserved type specimen. In this description, mention was made of the “remarkable” gill, in which the branchial plumes were described as “not very ample” (Eliot 1906a: 662).

Lim & Chou (1970) depicted, but did not immediately identify, a dendrodorid from Singapore. Their figure 9C, is instantly recognisable as *D. atromaculata* and their description (as *Dendrodoris* sp. 2) confirms this with the words “creamy-yellow with round black patches on the mantle” and “Gills ... consisting of 4 quadripinnate branches arranged at right angles to each other ... ” (see Lim & Chou 1970: 96-97). In an addendum to the manuscript, Lim & Chou (1970: 104) state that their *Dendrodoris* sp. 2 equals *Dendrodoris singaporensis* sp. nov., and that the type material was lodged in the Singapore National Museum. Unfortunately enquires at this institution did not result in location of this material.

Material Examined

India: HOLOTYPE Madras, Waltair; 1 specimen (35–40 mm living length, unknown date in 1853–4, coll. Sir Walter Elliot, (NEWHM: 1998. H4379), probably intertidal.

Australia, Queensland: Gulf of Carpentaria, 80 km west of Weipa; 1 specimen (42 mm preserved length), unknown date, coll. M. Gorman & C. Lu, (NMV Reg. No. F86791) depth 42 m; Rows Bay, Townsville; 1 specimen (67 mm long, live), 8 August, 1998, coll. G. Brodie (BC, J1); 1 specimen (85 mm long, live), 27 August, 2000, coll. J. Lariscy, (BC Z1); 1 specimen (54 mm preserved length), 16 September, 2001, coll. F. Chouw (BC K2); Myora Spit, North Stradbroke Island; 1 specimen (85 mm long, live), 4 October 1983, coll. R. Willan & O. Kelly (NTM Reg. No. P625).

Fiji: Viti Levu, Nasese, Suva, 1 specimen (37 mm long live), 26 December 1987, coll. G. & J. Brodie, BC D1 (intertidal).

Remarks on Type Material

As stated by Eliot (1906a), the holotype described by Alder & Hancock (1864) was originally collected by Walter Elliot in 1853-4. This specimen is lodged in the Hancock Museum at Newcastle-on-Tyne and registered under the system described by Eliot (1906b). When the material was re-examined by Eliot (1906a: 662) he stated that, although many of the Alder & Hancock specimens were in very poor condition, the holotype of *D. atromaculata* was “rather well preserved.” This holotype was examined in the current study. The specimen is indeed well preserved and the characteristic black notal markings can be clearly seen despite 150 years of preservation. The specimen has previously been dissected by an anterior dorsal incision. The internal organs are intact and appear in reasonable condition. Although the holotype is small (only 15 mm preserved length) compared with the material examined in the current study, I have no doubt that they belong to the same species because of the distinct external features and markings.

Redescription

The following description is based on the examination of four live specimens [BC - D1, J1, Z1 & K2], preserved material (including three specimens dissected and selectively sectioned [BC - J1, Z1 & K2] and two additional specimens [NTM P625, NMV F86791] used to supplement the histological investigation of the notum.

Dendrodoris atromaculata is tuberculate, possesses a relatively high body profile and is large and broad in comparison to several other members of the genus that are relatively smooth and elongate e.g. *D. nigra* (Stimpson, 1855). The extended crawling length of living adults is up to 85 mm. The body is soft but firm. The dorsum is covered in irregular “star-like” compound tubercles, each consisting of a cluster of finger-like papillae of different heights that taper to rounded apices (Figure 2A). The apex of these subsidiary papillae is often pinkish in formalin-preserved material and the central papilla is generally larger than the rest. A microscopic inspection of the remainder of the notum, between the tubercles and along the mantle edge, reveals a covering of simple papillae.

The notum is pale yellow, sometimes darkening to orange centrally. In the Fijian specimen, irregular ginger-brown patches were present, primarily around the notal margin (Figure 1B). These were not observed in the Australian material but replaced by a more even spread of large, irregularly-shaped black patches (Figure 1A). When these dark patches occurred close to a compound tubercle the pale apices of the papilla became even more obvious (because of the dark background), thus giving a distorted impression of an uneven distribution of tubercles over the notum.

In one specimen examined from Rowes Bay, small black spots were scattered across the ventral underside of the pale orange notum, but these markings were absent in the remaining specimens. Some dark markings from the dorsal surface were visible ventrally in some preserved material because of the translucent nature of the body tissue.

The fully retractable rhinophores are small and relatively inconspicuous for the size of

the animal. The clavus is orange, diagonally lamellate, and quite long proportionally. The stalk is translucent and there is no change in width or angle where the claval lamellae begin.

In all of the material examined, the cream and grey gill consists of four, large branchiae. When the living animal is at rest, these branchiae form a large equilateral cross over the rear of the body (see Figure 1A). The edge of the gill pocket is simple, without a raised rim. The anal papilla is not large or prominent and there is no sign of a gap between the posterior gill branchiae as seen in some other *Dendrodoris* species. Internally, large gill retractor muscles are found at the gill base and, as documented for *D. nigra* (see Wägele *et al.* 1999), these extend down between the posterior lobes of digestive gland before running along the ventral surface of the body cavity.

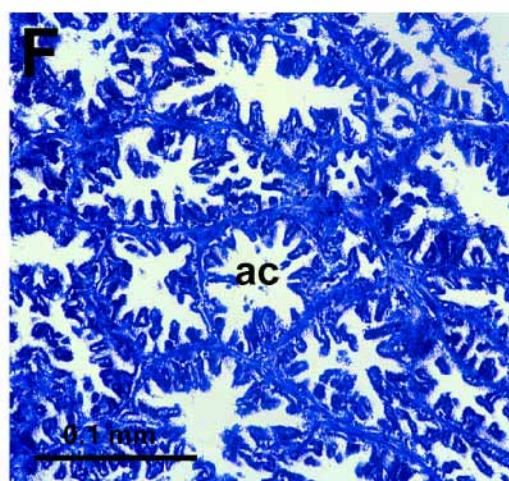
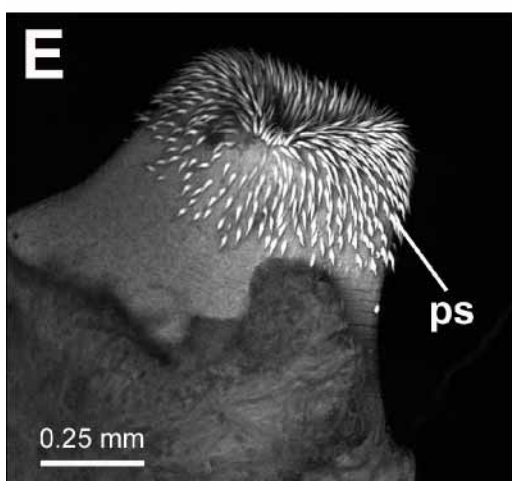
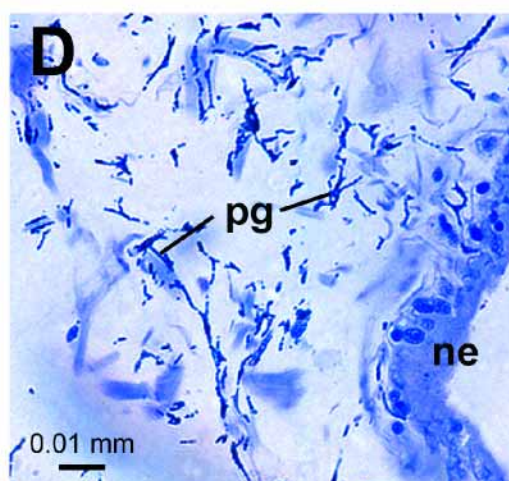
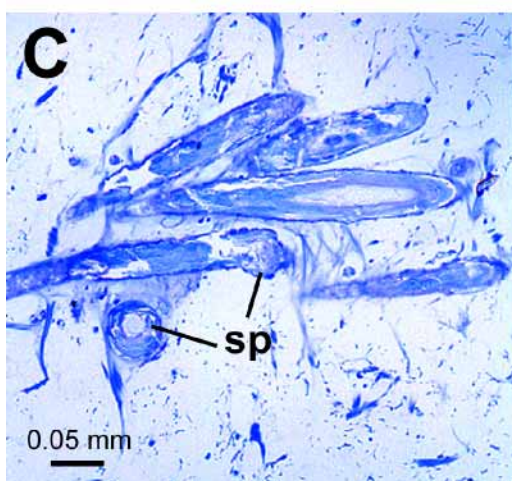
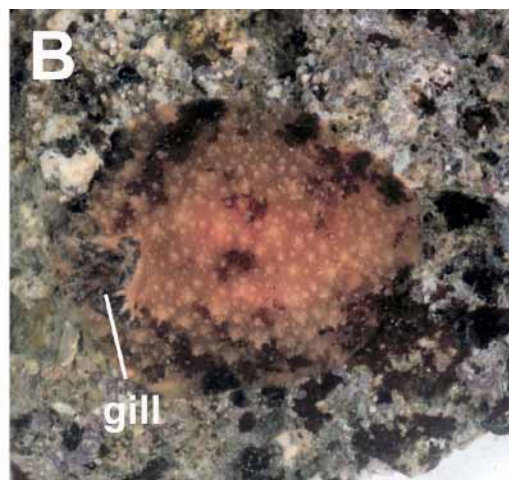
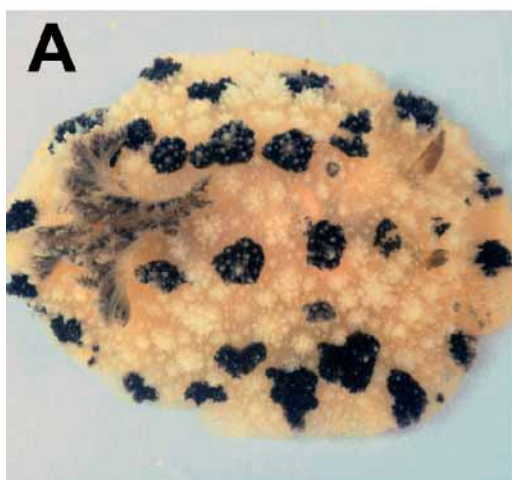
The notum overlaps the vivid orange foot by a considerable margin. However, the foot itself is large and quite wide (18 mm wide in 37 mm long animal), sometimes with small brown spots on the dorsal surface. The mouth is ventral, within a notch in the antero-ventral surface of the foot. No oral tentacles were observed in either live or preserved material.

General Histology

The large size of specimens precluded serial sectioning of the whole animal. However, sections of the notal tissue were examined from three specimens (two collected fresh at Rowes Bay one year apart, and another from North Stradbroke Island). Bundles of large (~0.3 x 0.04 mm), elongate spicules (Figure 1C) were located in the notal connective tissue. The notal tissue of all three specimens also contained unusual, microscopic, dark-staining structures forming thin, irregular lines (Figure 1D). At first these structures were thought to be fungi or bacteria. However, further analysis (using wax histology) gave a negative result for fungi (PAS stain, see methods section) and an inconclusive result for bacteria (Gram stain). In light of these results, I believe these structures to be black pigment within the connective tissue. However, this arrangement of pigment is quite different (very wide-spread throughout the tissue rather than concentrated along the notal epithelial boundary) to that seen in other members of *Dendrodoris* (e.g. see *D. nigra* in Wägele *et al.* 1999: Figures 1A & B).

Ciliated cells were not detected along the notal epithelium, nor were copiously vacuolated epithelial cells, as defined by (Wägele 1998), visible in the notal epithelium.

FIGURE 1A–F. Photographs of *Dendrodoris atromaculata* **A.** Living animal (67 mm live length) found intertidally at Rowes Bay, Townsville, Australia. Photograph by J. Brodie. **B.** living animal (37 mm live length) found intertidally at Nasese, Fiji. **C.** histological section showing spicules located in the notal tissue. **D.** histological section showing the unusual distribution of pigment in the notal tissue. **E.** confocal microscope scan of a semi-everted penis. **F.** histological section through the vestibular gland of the reproductive system showing rounded acini. ac = acinus, ne = notal epithelium, pg = pigment, ps = penial spines, sp = spicule.



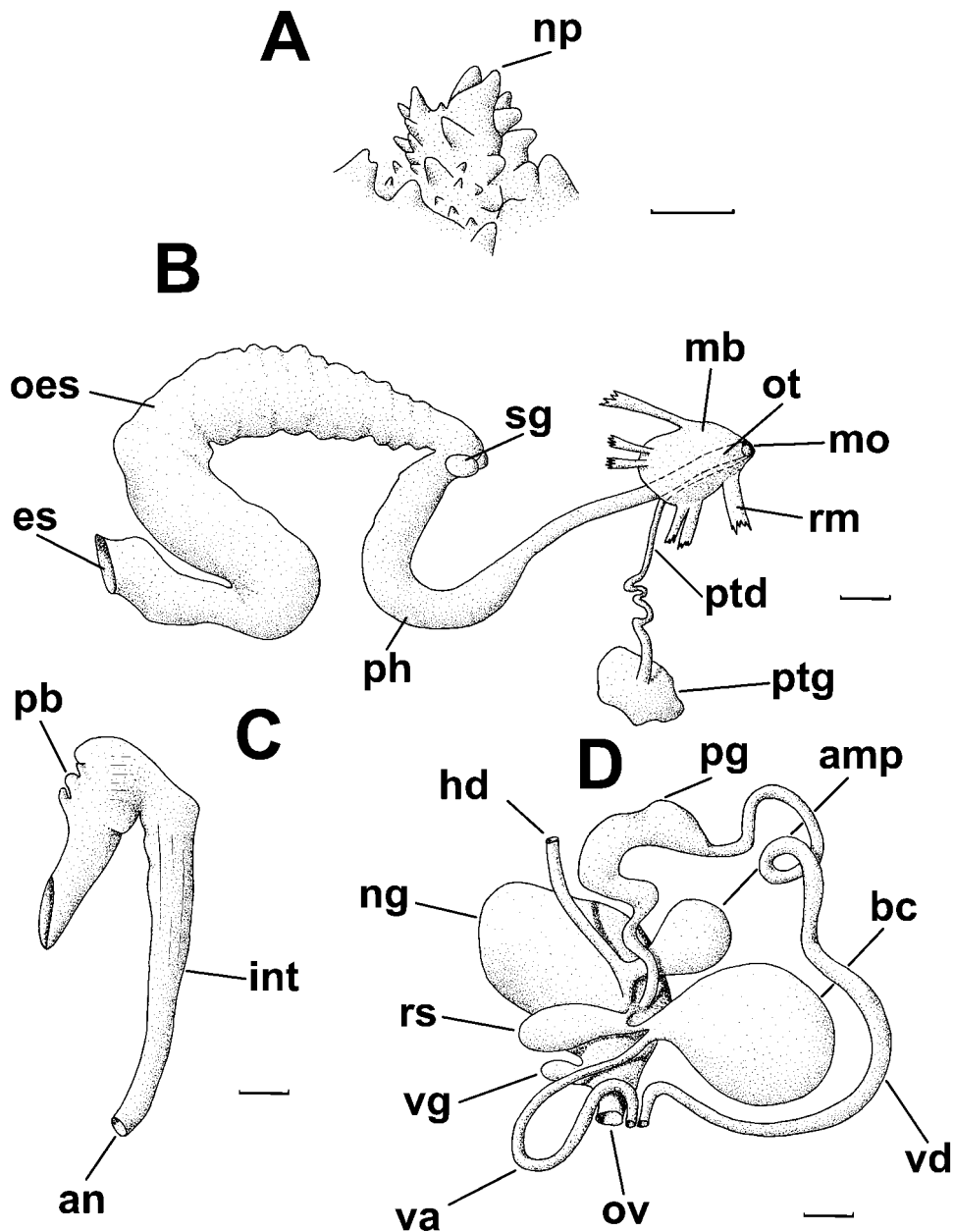


FIGURE 2 A–D. Composite drawings of *Dendrodoris atromaculata* (preserved material) showing: **A.** compound dorsal tubercle. **B.** anterior part of the digestive system. **C.** posterior part of the digestive system. **D.** arrangement of the post-gonadal reproductive system. amp = ampulla, an = anus, bc = bursa copulatrix, bw = body wall, es = exit to stomach, hd = hermaphroditic duct, int = intestine, mb = muscular bulb, mo = mouth, ng = nidamental gland, np = notal papilla, oes = oesophagus, ot = oral tube, ov = oviduct, pg = prostate gland, ph = pharynx, pb = pyloric bulb (not present in all individuals), ptd = ptyaline duct, ptg = ptyaline gland, rm = retractor muscle, rs = receptaculum seminis, sg = salivary gland, va = vagina, vd = vas deferens, vg = vestibular gland. Scale bars = 2 mm.

Digestive System

A diagram of the anterior part of the digestive system is given in Figure 2B. The ptyaline gland is not distinctly bilobed and the ptyaline duct is relatively long and thin, becoming very narrow distally. Distally, the ptyaline duct and the oral tube are both surrounded by a muscular bulb. The smooth pharynx is relatively long and a pair of rounded, compact salivary glands is present, at the junction of the pharynx and oesophagus, one on either side. The salivary glands are difficult to find in preserved material because their coloration is very similar to the pharynx on which they sit. The oesophagus is broad and bumpy in external appearance, particularly distally. It curves around on itself several times before entering the stomach within the pale brown digestive gland. As is typical of the genus, the stomach is indistinct and totally embedded within the digestive gland. The digestive gland is by far the largest organ in the body cavity, and very distinctly bilobed posteriorly.

The posterior part of the digestive system is simple with the intestine arising from the embedded stomach to emerge from the posterior half of the digestive gland. In only one of the three animals dissected, a pyloric bulb with several folds could be seen proximally (Figure 2C). No bulb or folds were seen in the two other specimens. The intestine is narrow, dorso-ventrally flattened and thin walled, it extends over the digestive gland before terminating at the anus. The anal papilla is not swollen and lying among the large gill branchiae remains inconspicuous.

Reproductive System

The vivid orange gonad was well developed in all three specimens dissected and covers most of the digestive gland. The post-gonadal reproductive system is shown in Figure 2D. The system is triaulytic with the rounded bursa copulatrix (= gametolytic gland) and elongate receptaculum seminis leading from the vaginal duct. The ampulla is simple and pyriform. The prostate gland is tubular and uniform in appearance. A rounded vestibular gland (~2 mm in diameter) is present within the body cavity and attached close to the base of the distal oviduct. The vas deferens is smooth and uniform in width; while the penis is armed with numerous rows of closely packed, elongate spines (Figure 1E).

Histology of Vestibular Gland

The vestibular gland contains large, rounded acini (Figure 1F) and the lumen has no epithelial fringe of deep staining microvilli known to house bacteria in some other *Dendrodoris* species (see Klussmann-Kolb & Brodie 1999). Additional wax sections of the vestibular gland were examined for bacteria, but none were detected by the Gram stain technique.

Nervous System

The nervous system is well developed with a ring of fused ganglia surrounding the distal pharynx. The smooth surfaced pharynx can move freely backwards and forwards

through this ring. A separate pair of small, cream ganglia is also located well behind this principal ring, very close to the salivary glands. Without close inspection, it is possible that these ganglia could be confused with the salivary glands.

Circulatory & Excretory Systems

The blood gland is irregular in shape and flattened dorso-ventrally. *In situ*, it lies dorsally over the anterior section of the oesophagus, just posterior to the ring of ganglia described above. A rounded renal syrinx is present and located on the right side, in the posterior-most section of the body cavity.

Occurrence and Habitat

Dendrodoris atromaculata appears to be relatively rare, a fact also noted by Alder and Hancock (1864). The type locality is Waltair, India. The field guide of Willan & Coleman (1984) records *D. atromaculata* as occurring in Queensland and Western Australia, however, the current study documents for the first time the presence of *D. atromaculata* in tropical Australia, Fiji and Singapore. The four living specimens observed in the current study were found in very shallow water at the lower section of the intertidal zone, either out in the open within sponge-gardens or under rocks on sheltered muddy reefal areas.

Natural History

No details of egg masses or developmental biology are currently known for this species. The Townsville specimens were found in consecutive years during the month of August. This may well suggest a seasonal occurrence, particularly since the large size and conspicuous appearance of this species should make it relatively easy to find. However, these collections may also be the result of increased accessibility to intertidal sponge gardens during the very low tides at this time of year. One individual found in Rowes Bay was observed to excrete orange faeces, strongly suggesting it had been feeding on an orange sponge. Compared with several other dendrodorids (e.g., *D. fumata* Rüppell & Leuckart, 1828) *D. atromaculata* is relatively inactive in captivity.

Diagnostic Features

Dendrodoris atromaculata is unique among described members of *Dendrodoris* being the only member of the genus known to possess finger-like notal papillae, large dense notal spicules and a gill plume that is cross-like. The distinguishing external features of *D. atromaculata* are its: (a) large size, (b) high body profile, (c) yellow ground colour (generally with black patches), (d) lack of oral tentacles, (e) finger-like papillae distributed over the notum, (f) “star-like” dorsal tubercles and (g) large cross-like gill plume. Internally, the distinctive features are: (h) an unusual distribution of black pigment within the connective tissue, (i) large, dense notal spicules, and (j) distinctive rounded acini within the reproductive vestibular gland.

Discussion of some important and previously used generic features and phylogenetic characters
Ptyaline Glands & Notal Spicules

Possession of ptyaline glands, unique digestive structures found in all members of *Dendrodoris*, confirmed the generic placement of *D. atromaculata*. However, the discovery of prominent notal spicules was unexpected since Valdés & Gosliner (1999) and Valdés (2002) found “integumentary” spicules were absent in all species of *Dendrodoris* included in their phylogenetic analyses of radula-less dorids and cryptobranch dorids respectively. An absence of such spicules can therefore no longer be considered as a generic feature for *Dendrodoris*.

Pyloric Bulb or Sac

In only one of the three animals dissected was a pyloric bulb (as defined by Wägele *et al.* 1999: 92) present (see Figure 2C). These findings confirm the intraspecific variation of this intestinal structure, as previously found by Brodie *et al.* (1997) [described under the incorrect term pyloric gland], and confirms that the presence and form of a pyloric bulb (or sac) is unsuitable for separating species and for use in phylogenetic analyses.

Vestibular Glands

The vestibular gland microstructure found in *D. atromaculata* has, to date, been found only in an unnamed species of *Dendrodoris* from Japan (see Brodie 2002). Relatively few *Dendrodoris* are known to possess a vestibular gland (e.g., *D. nigra*, *D. goani* Rao & Kumary, 1973; *D. elongata* Baba, 1936). However, vaginal glands sometimes also called vestibular glands (see Gosliner 1994) are reported from many dorid nudibranchs. Description of these reproductive accessory organs has largely been undertaken at the gross morphological level (Gosliner 1994) with little description of ultrastructural detail or microanatomy. This fact makes the collective usage of “presence or absence” of such glands, at the gross morphological level in phylogenetic studies, inadvisable because ultrastructural or microanatomical investigation is required to determine their similarity. This conclusion is reinforced by the vestibular gland investigations of *D. nigra* (see Klussmann-Kolb & Brodie 1999), where an unusual microstructure was found to house symbiotic bacteria, and in similar investigations of *D. coronata* Kay & Young, 1969 (see Brodie & Klussmann-Kolb 2000) and *D. fumata* (Rüppell & Leuckart, 1828) (see Brodie 2001). In the latter two species, the vestibular gland is embedded within the body wall making it non-observable by gross dissection. In future comparative studies it is essential that microstructural investigations of these organs, and the surrounding body wall tissues, be undertaken.

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